Spatial organization and strategy of habitat utilization of elephants in Tsavo National Park, Kenya[1]

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1 Introduction

The drastic and widespread modification of the original woodland vegetation of Tsavo National Park, mainly through the activities of large numbers of African elephants, *Loxodonta africana* (Blumenbach), has caused considerable concern among conservationists for quite some time (e. g. Napier Bax and Sheldrick 1963; Glover 1963; Laws 1969a; Leuthold 1969). It led to the establishment of the Tsavo Research Project in 1966, with the objective of investigating various aspects of the "elephant problem". Unprecedented elephant mortality in 1970/71 (Corfield 1973) triggered renewed and intensified research into elephant ecology, as earlier studies had left many questions unanswered.

The more important among these concerned the total range and the internal organization of the Tsavo elephant population, as well as the seasonal movements of individuals and groups, and the environmental factors governing them. Laws (1969a) had concluded that the elephants of the Tsavo area were organized into ten discrete "unit populations" inhabiting separate ranges and performing at most limited seasonal movements. This conclusion was based on about one year's field work involving mainly large-scale aerial surveys but no records of individually known animals; various casual observations provided grounds for doubting its general validity.

Against this background the present study was initiated with the main aims of obtaining information on movements of individually known elephants and their relations to environmental factors, and attempting to relate individual movements to changes in spatial distribution of the overall population. An additional objective was to determine the ecological significance of the park boundaries for the elephants, and the influence of changes in land use and human activities in areas adjacent to the park.

The study began in December 1971 and continued, with varying intensity, until early 1976. A preliminary paper (Leuthold and Sale 1973) dealt with the results of the first year; the following is a comprehensive report on the entire period of study.

2 Study area and methods

2.1 The study area

Tsavo National Park (ca. 20.000 km^2) is situated in south-eastern Kenya, in a semi-arid area originally covered mainly by dry woodlands dominated by *Acacia* and *Commiphora* spp. The Nairobi—Mombasa road and railway line divide it into two parts administered as

[1] Dedicated to the memory of David Sheldrick, who devoted his life's work to the Tsavo elephants.

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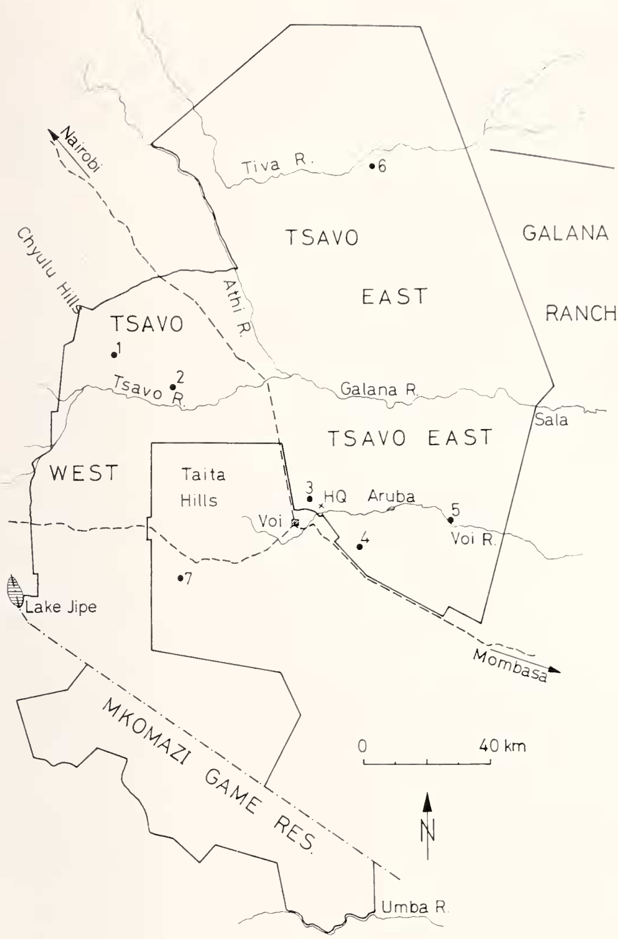

Fig. 1. Map of Tsavo National Park and vicinity ——— = Boundary of national park and Mkomazi Game Reserve; · — · — · = Kenya/Tanzania border; — — — = main roads and railway lines Mombasa-Nairobi and Voi-Taveta-Arusha; ● = artificial water supplies: 1 = Kilaguni Lodge; 2 = Ngulia Safari Lodge; 3 = Voi Safari Lodge; 4 = Ndara borehole; 5 = Mukwaju borehole; 6 = Ndiandaza borehole; 7 = Taita Hills and Salt Lick Lodges (outside the park); HQ = Park headquarters and research station

separate units, Tsavo West (ca. 7.000 km²) and Tsavo East (ca. 13.000 km²; Fig. 1). Their main features have been described repeatedly (e. g. Napier Bax and Sheldrick 1963; Laws 1969a; Leuthold and Sale 1973); in the present context, the following are most relevant:

Physiography: Tsavo West, particularly its northern portion, is considerably more varied in topography and geology, including the Ngulia Hills (up to 1.800 m a. s. l.), the extremities

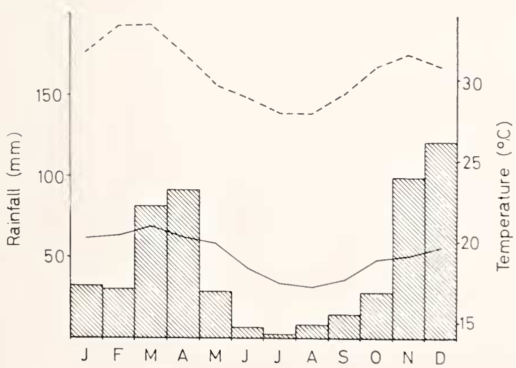

Fig. 2. Mean monthly rainfall (66-year average in mm) and mean monthly maximum (— — —) and minimum (______) temperatures (31-year average in °C) at Voi town. Data from East African Meteorological Department

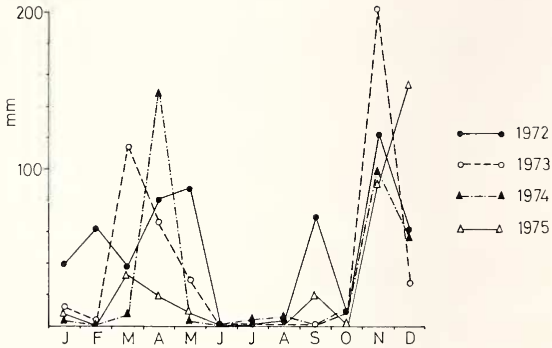

Fig. 3. Monthly rainfall (in mm) for 1972—1975 at Tsavo East Research Station, showing year-to-year variations

of the Chyulu Hills (up to 2100 m) and several extensive lava flows covered by partly evergreen vegetation. Tsavo East, by contrast, is mostly flat (300—500 m a.s.l.), except for some isolated granitic hills in the west and north, and geologically much more uniform.

Climate: Mean annual rainfall is ca. 550 mm at Voi town, just outside the park (Fig. 1), somewhat more in northern Tsavo West, and slightly to considerably less in southern Tsavo West and most of Tsavo East. The annual mean for 1969—1975 at both Aruba and Sala (Fig. 1) was about 260 mm. Most rain falls in two rainy seasons, the main one being in November/December, followed by a short but hot dry season January—March); another rainy season occurs in March—April (—May), and the period June—October is generally dry and relatively cool, with temperatures rising again in September/October (Fig. 2). This long dry season is the main period of stress for herbivores, including the elephant, as strong southerly winds desiccate soil and vegetation, exacerbating the lack of rainfall.

While the seasons described are reasonably well-defined on average (Fig. 2), rainfall varies substantially in its spatial and temporal distribution (Fig. 3). The rains may "fail" to varying degrees in one season, or considerable rain may fall "out of season"; some areas may receive substantial rainfall from isolated thunderstorms, while others remain completely dry. This makes it difficult to delimitate the seasons, as conditions may differ considerably between different areas at any one time. Occasionally, some subjective judgement was necessary to assign a given date to either the rainy or the dry season; in addition there are, of course, transitional periods. In most years, the two dry seasons combined are longer than the two rainy seasons (6—8 vs. 4—6 months).

Water: Numerous shallow pans hold water after the rains; once they dry out, open water is available only at a few permanent natural water supplies and some artificial ones added in recent years (see Ayeni 1975). The Athi, Tsavo and Galana Rivers usually flow the year round. Smaller rivers (e. g. Voi, Tiva, etc.; Fig. 1) retain stagnant pools and ground water throughout the dry season; elephants can reach the latter by digging holes in the sandy river beds. In southern Tsavo West water is permanently available at Lake Jipe (Fig. 1). The Aruba Dam in Tsavo East stores water of the Voi River throughout the dry season. Kilaguni, Ngulia and Voi Safari Lodges have artificial water supplies, and at three boreholes in Tsavo East ground water can be pumped up during the dry seasons (Fig. 1).

Overall, northern Tsavo West is probably the most "favourable" area ecologically, because of its varied topography, geology and resultant diversity of vegetation, as well as the numerous springs around the lava fields emanating from the Chyulu Hills. In southern Tsavo West and in most of Tsavo East environmental conditions are generally harsher (Cobb 1976). Much of Tsavo East is also subject to periodic droughts with less than 250 mm annual rainfall. This study immediately followed the drought of 1970/71 (see Corfield 1973) and included several relatively dry years, particularly 1974 and 1975.

2.2 Methods

Data were collected at two levels:

1. Recording of overall distribution patterns by aerial total and sample counts, primarily as background information;
2. determination of movements and home ranges of individual elephants, by reference to visually identifiable animals and by radio-tracking of selected individuals.

2.2.1 Overall distribution patterns

Aerial total counts were carried out in Tsavo Park repeatedly since the "elephants problem" became acute (e. g. Glover 1963; see also Leuthold 1976a). During the present study, two total counts were conducted, in September 1972 and January 1973 (discussed by LEUTHOLD and SALE 1973).

From August 1973 to March 1975 eight systematic aerial sample counts were carried out at intervals of 2—3 months. North-south transects were flown, 10 km apart, over a total area of about 40.000 km^2; all large mammals seen within a strip of predetermined width were recorded and the results expressed as densities in 10 × 10 km grid squares (see COBB 1976).

2.2.2 Home ranges and movements of individual elephants

2.2.2.1 Visual identification

Many elephants can be recognized individually from natural characteristics such as broken or unusually shaped tusks, cuts or holes in the ears, etc. (cf. DOUGLAS-HAMILTON 1972). Photographs of such elephants were mounted on file cards, together with a detailed description, date and locality of the first sighting, as well as group size and composition. Marginal punches referring to the individual characteristics facilitated subsequent identification of known animals. During drives along the park roads I scrutinized all elephants seen for the presence of known or recognizable individuals. Because of the park's size and the rough terrain, these observations were limited to the southern Tsavo East, the area south of the Galana River (ca. 4.150 km^2; Fig. 1).

However, the rate of resightings of known individuals was very low in relation to the aims of the study and the effort and expense involved (time, vehicle running costs, etc.). This was mainly because the number of known individuals was small, compared to the total number of elephants normally present in the area (ca. 6.000; LEUTHOLD and SALE 1973), and because known individuals were not always near a road where observations normally began. In the end, the information obtained served mainly to confirm and complement that derived from radio-tracking.

2.2.2.2 Radio-tracking

To overcome the limitations of visual identification and to be able to — ideally — locate any known individual at virtually any time and place, some 25 elephants were captured and equipped with radio-transmitters in different parts of the park. They were immobilized with etorphine hydrochloride ("M-99", commercially available as "Immobilon", with antagonist "Revivon", from Reckitt and Sons, Ltd.), administered with standard "CapChur" equipment (Palmer Co., Douglasville, Ga., USA). Radio transmitters, each with its own frequency, and receivers were obtained from the AVM Instrument Co. (W. W. Cochran), of Champaign, Ill., USA. Transmitters and batteries, embedded in dental acrylic, were attached to a collar made of two layers of machine belting (10 cm × 5 mm), which was fitted tightly around the elephant's neck and fastened with steel bolts set in steel plates. Tracking was done from a Piper SuperCub aircraft with a single three-element Yagi antenna mounted on a wing strut, pointing forward. Receiving range varied considerably between transmitters and was also influenced by local topography, the animal's position with respect to the aircraft, and by height above ground. Signals of the best transmitters were detected up to 70 km away at about 500 m above ground. Directional reception permitted the pilot to "home in" on instrumented animals, which were identified visually on most occasions. Locations were plotted on 1:250.000 maps; in featureless country they had to be determined by compass bearings and flying time to a known landmark and are, therefore, only approximate in some cases. Due to the costs involved, and sometimes for technical reasons, instrumented animals could not be located as often as would have been desirable, nor on a strictly systematic timetable. On average, tracking was attempted once a week during the dry season, and twice a week during the rainy season, when the propensity for movements was highest. Various instances of damage to, or malfunction of, transmitters and/or antennas caused temporary or total loss of radio-contact. The longest life of a transmitter battery package was 22 months; in two cases new transmitters could be placed on animals whose original ones had ceased working.

Home ranges were determined by the "periphery method": the most peripheral locations of an animal were connected by straight lines, and the area thus enclosed was measured with a planimeter. This method gives no indication of the intensity and temporal pattern of utilization of a home range, and the areas thus determined may be considerably larger than those normally utilized by the animals concerned. On the other hand, home ranges of various large mammals have been derived in the same way, which facilitates comparison between species.

3 Results and discussion

3.1 Overall distribution patterns and their changes

From qualitative observations it had long been known that the Tsavo elephants tended to concentrate near permanent water supplies during the dry season; the original woodlands had therefore been damaged most severely near rivers such as the Galana, Voi and Tiva in Tsavo East (see Map 1 of Napier Bax and Sheldrick 1963). Also, large local aggregations of elephants during the rainy season had been noted repeatedly, particularly near the eastern park boundary in southern Tsavo East, where herds of several hundred, occasionally over a thousand elephants formed almost every year and then dispersed again (cf. Figs. 4 and 5 in Leuthold and Sale 1973).

The series of aerial sample counts carried out between 1973 and 1975 provided more quantitative information on distribution patterns, as well as on total numbers. The main advantages of these "monitoring flights" over the earlier total counts were 1. stricter control of methods and thus better repeatability (important with respect to total numbers); 2. their frequency, which permitted monitoring shifts in distribution at relatively short intervals; 3. simultaneous recording of environmental conditions, which made it possible to investigate the factors underlying such shifts; and 4. the fact that large areas outside the park were included in the counts, which made it reasonably certain that the total range of the Tsavo elephant population(s) was covered.

Cobb (1976) presented and discussed the results of these aerial counts in some detail; the following is a summary of the aspects most relevant in the present context:

1. *Seasonal changes in distribution.* In the dry season, elephants are essentially restricted to broad belts along the main rivers (Tsavo/Athi-Galana, Tiva). In the wet season a general shift to the north-east occurs in northern Tsavo East, into areas without permanent water supplies. In southern Tsavo East elephants occupy the easternmost areas in the wet season, retreating from them in the dry season, generally westwards toward the Aruba Dam and Voi. In southern Tsavo West there is a marked wet-season dispersal into the southern "arm" of the park; in the dry season those elephants move to the vicinity of Lake Jipe in the west and toward the Umba River in the south (Fig. 4).

2. *Causal relationships.* Using the environmental data recorded during the aerial counts Cobb (1976) attempted to determine correlations between habitat conditions and observed distributional changes by means of multiple regression analysis. For

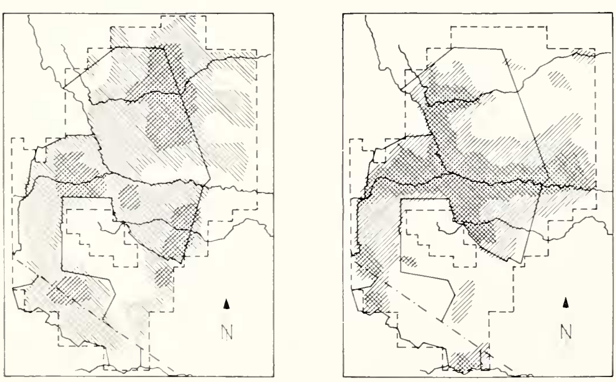

Fig. 4. Wet-season *(left)* and dry-season *(right)* distribution of elephants in the Tsavo area (after Cobb 1976). Cross-hatching indictates areas of highest density; absence of hatching does not necessarily mean total absence of elephants. — — — = Boundary of census area

various reasons this proved rather difficult, but some relationships were found that agree well with conclusions derived from more qualitative observations. For instance, dry-season distribution was negatively correlated with distance from permanent water in three of the four local subdivisions. In the wet season, high densities outside the park were associated with dense grass cover (West) and green grass condition (East). This can be interpreted as indicating that elephants moving out of the park (see below) select areas with, among other things, abundant grass in the wet season.

3. Movements across park boundaries. Large areas outside the park are occupied by elephants seasonally or permanently. The Mkomazi Game Reserve to the south and the Galana Ranch to the east (Fig. 1) offer protection similar to that in the park itself, but large unprotected areas are also important for the elephants, at least seasonally, e.g. in the north-east and in the south-east of the census area (Fig. 4). In the areas outside the park wet-season densities tended to be higher than dry-season ones, suggesting dispersal of elephants out of the park during the wet season (the differences were, however, not significant). Overall densities were considerably lower outside than inside the park, but all areas outside are not equally available or accessible to elephants.

4. Regional differences within the park. Overall elephant density was higher in the west than in the east generally. In northern Tsavo West, there were no noticeable changes in elephant distribution between the seasons (Fig. 4). This confirms the general statement made earlier (sect. 2.1) that Tsavo West, particularly its northern part, is ecologically more varied and thus more "favourable" for the elephants than most of Tsavo East. These environmental differences were investigated in some detail and quantified by Cobb (1976), who used them as the basis for regional subdivision of the total census area.

3.2 Individual home ranges

3.2.1 Observations on visually identified elephants

A total of 46 ♂♂ and 79 ♀♀ were photographed and recorded on file cards for subsequent identification. Of these, 25 ♂♂ (54%) and 44 ♀♀ (56%) were resighted at least once. As nine of the ♀♀ appeared to be permanently associated with other known individuals, ♀♀ will be discussed in the following in terms of "family units" (Buss and Smith 1966) rather than individuals (n = 35 resighted units). Only 13 ♂♂ (52% of those resighted at all) and 15 ♀♀ (43%) were seen more than four times, the minimum considered necessary to warrant at least a tentative determination of home ranges. The maximum number of sightings of a known individual was ten, over a period of 22 (1 ♂) and 24 (1 ♀) months, respectively. Most of these observations were made between early 1972 and early 1974.

Tables 1 and 2 summarize the information obtained through visual identification (in southern Tsavo East only!) and Figure 5 illustrates the positions and shapes of six home ranges. A few other home ranges were extremely narrow, almost linear, and their areas

Table 1

Distances between extreme locations of visually identified elephants

	Distance (km) 0—30	30—60	> 60	Number of animals
♂♂	18	5	2	25
♀♀	26	9	—	35

Table 2

Home range data for visually identified animals with at least four sightings

Area (in km²) and greatest diameter (in km) of home ranges

	Area (km²)			Diameter (km)		
	Mean	Range	n[1]	Mean	Range	n
♂♂	303	41—469	7	34.5[2]	3—67	13
♀♀	281	50—775	11	34.1	15—57	15

[1] Area not determined if home range nearly linear in shape. — [2] If two cases of only 3 km and 8 km are excluded, the mean rises to 39.7 km (n = 11)

were therefore not measured; hence the differences in the number of animals between the left- and right-hand parts of Table 2.

The following points emerge from these data:

1. Individual home ranges overlap considerably, both among ♂♂ and ♀♀, and between the sexes.
2. The main directions of elephant movements observed were NNW — SSE, parallel to the western park boundary (Fig. 1), or approximately N — S in the area between the Voi and Galana Rivers. Substantial movements in an E — W direction were recorded almost exclusively in the area south of the Voi River, mainly in the contex of the formation and dissolution of seasonal aggregations in the south-eastern corner of the study area (see sect. 3.1 and 4.1).

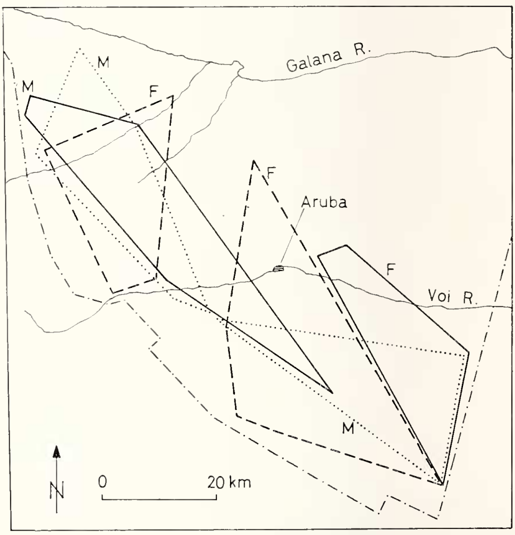

Fig. 5. Home ranges of six visually identified elephants (3 ♂♂, 3 ♀♀) in the area south of the Galana River. M = ♂; F = ♀

3. Within the period of observation, 16 (= 27 %) of the elephants resighted at least once moved over more than 30 km, which Laws (1969 a) considered to be the upper limit of seasonal movements (though he spoke of entire "unit populations" rather than individuals). There was little difference in this respect between ♂♂ and ♀♀, although two ♂♂ moved over more than 60 km (maximum 67 km; Table 2). Considering the small number of sightings obtained and the fact that no ground observations were made north of the Galana River, movements of individual elephants could have been even more extensive than those actually recorded.
4. At least five known elephants (3 ♂♂, 2 ♀♀) moved from the presumed range of one "unit population" (Text-Fig. 2 of Laws 1969a) well into that of another one (cf. Fig. 6 of Leuthold and Sale 1973). This suggests that the unit populations and their ranges, if real at all, are unstable in space and time. We shall return to this point below.

3.2.2 Radio-tracking

This section will review and discuss the information obtained from 21 radio-instrumented elephants (7 ♂♂, 2 ♀♀ in Tsavo West, 4 ♂♂ and 8 ♀♀ in Tsavo East; all in different groups originally) in relation to the influences of various environmental and other factors.

A few additional animals were equipped with radio-collars at different times but, for various reasons (mainly technical failures), did not provide any useful information and are therefore disregarded.

3.2.2.1 Size and shape of individual home ranges

Figure 6 shows the locations and shapes of home ranges of 11 ♂♂, Figure 7 those of 10 ♀♀ in both Tsavo East and West. Table 3 summarizes data on home range size and greatest linear dimensions, and deteils are given in Table 4, including the number of records for each individual and the period over which they were obtained. The latter was rather short in several cases, particularly in Tsavo West, and some caution is necessary in interpreting the data available.

In two cases the method of home range determination deviated slightly from that generally used in that allowance was made for the fact that the elephants concerned were never recorded west of the Nairobi-Mombasa road. Their home ranges therefore appear somewhat "dented" (M-11 in Fig. 6, F-18 in Fig. 7). Observations on these and some of the visually identified animals suggested that the road and railway line constituted a fairly effective barrier to elephant movements, though certainly not an absolute one. Only one of the radio-tracked individuals definitely crossed them (M-5, Fig. 6). However, unmarked elephants were repeatedly seen crossing the road; the reaction to road and railway line probably varies with individual experience and/or tradition within groups. (The home range of M-6 in Figure 6 is rather unrealistic, as depicted; the few records obtained fortuitously made it fall mainly outside the park.)

The graphic representation of home ranges in Figures 6 and 7 confirms some of the tentative conclusions drawn from the observations on visually identified elephants: Home ranges overlap extensively within and between sexes, and north-south movements are generally more prominent than east-west ones, the latter being most marked near, and to the south of, the Voi River (M-12, F-12, F-15). It further shows that very narrow, almost linear home ranges are rather exceptional (that of M-6 in Tsavo West is based on only five records).

In Tsavo East, all home ranges except one (F-11) were considerably larger than those determined through visual identification; in addition, four animals captured south of the Galana River all moved to the north of it several times. In fact, the greater parts of

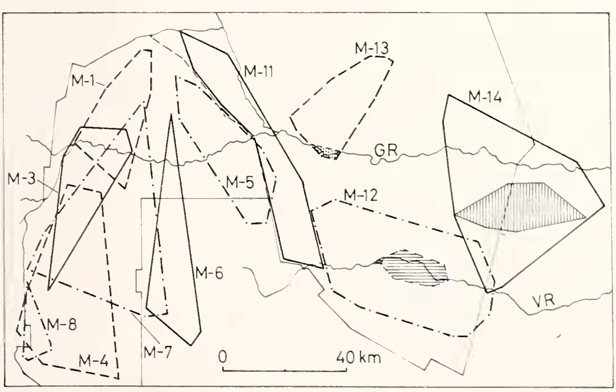

Fig. 6. Home ranges of 11 male elephants, obtained by radio-tracking. Shaded = dry-season ranges (see text)

the home ranges of F-13 and F-14 were located north of the Galana River (Fig. 7). These findings emphasize the inadequacy of the visual-identification method under the circumstances prevailing (size of the area, difficulty of access to certain parts).

The greatest distance between locations of the same animal exceeded 50 km in most cases, reaching a maximum of 75 km in Tsavo West (M-6) and 133 km in Tsavo East (F-13). It was less than 30 km in only two cases, both in Tsavo West (M-8 with a tracking period of only 2.5 months, and F-2; see Table 4).

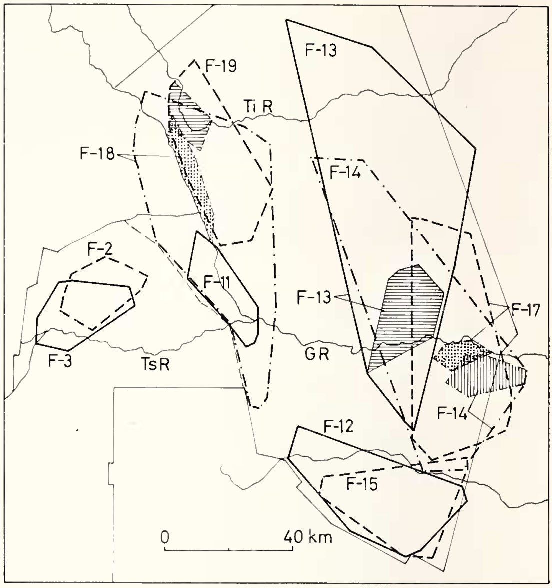

Fig. 7. Home ranges of ten female elephants, obtained by radio-tracking. Shaded = dry-season ranges (see text)

The data in Table 3 suggest considerable differences in home range size between ♂♂ and ♀♀, but while home ranges of ♂♂ were larger than those of ♀♀ in Tsavo West, the reverse was true in Tsavo East. None of these differences are however, statistically significant, and they may simply reflect the fortuitous choice of individuals for radio-instrumentation.

3.2.2.2 Procedural factors affecting home range sizes obtained

To investigate the influence on apparent home range sizes of factors related mainly to the method and circumstances of data collection rather than to environmental conditions, I proceeded as follows:

Table 3

Summary of home range data obtained by radio-tracking

Mean values for area (km²) and greatest diameter (km)

	Area (km²)	Greatest diameter (km)	n
Tsavo West — ♂♂	843	56.3	7
Tsavo West — ♀♀	408	32.0	2
Tsavo West — all	746	50.9	9
Tsavo East — ♂♂	1182	63.2	4
Tsavo East — ♀♀	1812	77.4	8
Tsavo East — all	1602	72.7	12
All ♂♂	966	58.8	11
All ♀♀	1532	68.3	10
All combined	1235	63.3	21

Table 4

Radio-tracking data on individual elephants in Tsavo National Park

Animal No.	Year	Period under obs. (months)	No. of records	Maximum distance (km)	Size of home range (km²)	Notes
			1. Tsavo West			
M— 1	72	5.5	81	46	594	
M— 3	72	4	22	57	691	1
M— 4	74/75	4	17	66	1503	
M— 5	74/75	6	34	55	608	2
M— 6	75/76	1.5	5	75	684	
M— 7	75/76	3	15	70	1673	
M— 8	75/76	2.5	15	25	146	
F — 2	72/73	13.5	64	29	369	
F — 3	72/73	9	48	35	448	1
			2. Tsavo East			
M—11	72/73	10.5	35	90	822	1
M—12	72/75	37	160	65	1640	1,3
M—13	73/75	18	74	36	516	1,3
M—14	74/75	11	63	62	1750	4
F —11	72/73	6	24	40	387	5
F —12	72	4	20	57	1238	1
F —13	72/73	16.5	76	133	3744	
F —14	72/73	13.5	60	105	2975	
F —15	73/74	3	16	50	974	
F —17	74/76	19	97	75	1720	
F —18	74/76	18.5	101	102	2452	
F —19	74/75	12.5	66	57	1009	4

Notes: 1 = gap(s) in tracking records, usually due to (temporary) transmitter failure; 2 = 3 sight records after 3 months within same home range; 3 = two transmitters used consecutively on same animal; 4 = killed by hunters (M-14) or poachers (F-19) while transmitter was still functioning; 5 = moved away from original area and later "settled down" elsewhere

Firstly, I calculated correlation coefficients between individual home range sizes and the number of records on the one hand, and period of tracking on the other hand, for ♂♂ and ♀♀ separately in Tsavo West and East, and for all animals in Tsavo East. However, in no case were the correlations significant.

Secondly, I mapped all radio-locations in chronological sequence and determined individual home range sizes after every ten records (i.e. after 10, 20, 30, etc.). The values obtained for each of the eight animals with the largest numbers of records (3 ♂♂ and 5 ♀♀ in Tsavo East only) were plotted over a time axis. The resultant curves (Fig. 8), mostly of a generally sigmoid shape, illustrate the relationship of home range size to both time and number of records. They indicate that (a) these relationships vary considerably between individuals, and (b) that a prolonged period of time is necessary to provide a reasonable indication of an elephant's total home range (of course, the data presented here may themselves not be definitive!). Whereas one year's tracking appeared to be sufficient in some cases (e.g. F-13, F-14, F-18), this did not apply to other animals (e.g. M-12, F-17). However, in M-12 home range size did not increase further after slightly over 1.5 years with about 100 records, despite continuation of tracking for another year. Thus, while it is difficult to derive general rules regarding the minimum tracking period necessary for conclusive results, the data available suggest that at least 1—1.5 years are

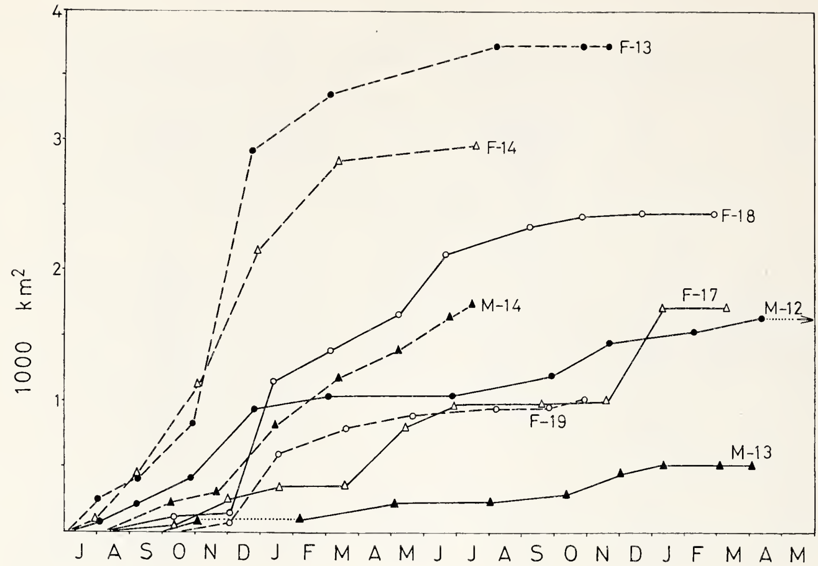

Fig. 8. Increase in size of individual home ranges over time. Each point indicates home range size after 10, 20, etc. radio-locations (which were obtained at irregular intervals), plotted over a time scale in which several years' records are combined

required (this requirement may, of course, vary with the environmental conditions in other study areas). Home ranges obtained from substantially shorter tracking periods must be considered as provisional; in the present study this applies to all but one of the individuals in Tsavo West, and to at least three in Tsavo East (see Table 4). This proviso has to be kept in mind in the following discussions.

3.2.2.3 Ecological factors influencing home range size and utilization

The seasonal changes in overall distribution of elephants (Fig. 4) as well as various casual observations indicate considerable seasonal variations in habitat utilization. The lack of open water in large parts of the park virtually precludes their use by elephants during the dry seasons, and the elephants are compelled to concentrate within reach of permanent water supplies. These seasonal changes are also reflected in the pattern of utilization of individual home ranges (see Fig. 3 in Leuthold and Sale 1973). For several elephants, particularly in Tsavo East, marked local concentrations of radio-tracking records clearly indicated areas used primarily during the dry seasons.

For present purposes I determined the smallest portion of each individual's home range that included 50% of all records (shaded areas in Figs. 6 and 7). As they contained almost exclusively dry-season records, the areas thus determined are probably representative of the "dry-season ranges" of individual elephants (and their groups). In the cases considered here (eight animals in Tsavo East), they comprise about 10% of the total home ranges, with marked individual variation from about 2% in M-13 to ca. 23% in M-17 (Fig. 6). As expected from other observations (cf. Fig. 4), these dry-season ranges are all located relatively near one of the permanent water supplies (Galana River for F-13, F-14, F-17, M-13 and M-14; Voi River and Aruba Dam for M-12; Athi River for F-18; upper Tiva River for F-19).

We may therefore conclude that elephants in Tsavo East utilize only small, favourably located portions of their overall home ranges during the dry seasons and move to other parts mainly during the rainy seasons. This is borne out to some extent by the data on the increase of home range sizes over time (Fig. 8). Most individual home ranges "grew" most markedly during the rainy seasons, i.e. in November/December and, to a lesser extent, in April/May.

Dry-season ranges of elephants in Tsavo West could not be determined in the same manner because the data obtained there were insufficient (see Table 4). Some casual observations and the data from the monitoring flights suggest that the situation is similar there, with Lake Jipe, the Tsavo River and the lava flows emanating from the Chyulu Hills (Fig. 1) providing permanent water supplies on which dry-season ranges are based.

Apart from these seasonal variations in the utilization of individual home ranges there are differences in mean home range size between Tsavo East and Tsavo West. Figures 6 and 7 suggest that home ranges are larger in Tsavo East, most markedly in ♀♀. There appear to be certain gradients in home range size, which is smallest in northern Tsavo West, somewhat larger in southern Tsavo West, southern Tsavo East, north-western Tsavo East, and largest in eastern Tsavo East. If ♂♂ and ♀♀ are compared separately, differences between Tsavo East and West are not significant ($p \geqslant 0.05$), but the mean size of all home ranges in Tsavo West is significantly smaller than in Tsavo East (Student's t-test; $p < 0.05$). While these differences, being based on small samples of subjectively selected animals, should not be overrated, they are nevertheless plausible when related to ecological conditions. As stated earlier, northern Tsavo West is the most favourable area, with a broken topography, higher rainfall, more varied vegetation and numerous springs along the edges of lava fields (see also Cobb 1976). This can explain the fact that home ranges of elephants captured in that area were all among the smallest recorded (M-1, M-3, F-2, F-3; see Table 4). Environmental conditions are less favourable in the other areas, in the approximate order of those enumerated above, reaching their extremes in north-eastern Tsavo East.

While other factors undoubtedly play their part, rainfall is probably the main single determinant of environmental conditions. Figure 9 shows the spatial distribution of rainfall during the climatic year July 1973 to June 1974 (Cobb 1976), which can probably be considered as representative of the rainfall pattern in general, even though this varies greatly from year to year. According to these data, most of northern Tsavo West received 500 mm or more rain during the period considered. The north-western and southern portions of Tsavo East are ecologically allied to Tsavo West, also receiving relatively high rainfall, compared to the major portion of Tsavo East, particularly the north-eastern parts, with an annual total of only 250 mm or less (Cobb 1976).

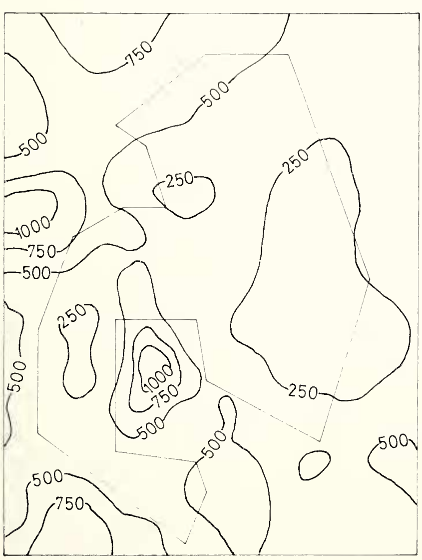

Fig. 9. Spatial distribution of rainfall in the Tsavo area for the climatic year July 1973 to June 1974. Isohyets at 250-mm intervals (after Cobb 1976)

Comparison of Figure 9 with Figures 6 and 7 suggests an inverse relationship between annual rainfall and the size of elephant home ranges within the study area. It is, however, difficult to express this relationship in quantitative terms; possible reasons for this difficulty include 1. the relatively small data base, 2. the problem of obtaining adequate rainfall records for many locations, and 3. the practical impossibility of collecting radio-tracking data on a strictly systematic schedule. In addition, factors other than rainfall can, of course, also influence home range size in elephants, e.g. permanent water supplies, soil and vegetation types, the severity of seasonal changes in food and water supplies, etc. It may therefore be unrealistic to expect a straightforward quantitative relationship between home range size and rainfall, even though such a relationship appears fairly obvious qualitatively. Rainfall, of course, does not act directly on the elephants, but through its effects on quantity and quality of the food supply.

3.3 Movements

A feature of the radio-tracking data were occasional sudden movements of individual elephants (and their groups in the case of ♀♀) over distances of 30—50 km, or even more, within a few days. Most of these are plotted in Figure 10, with a few exceptions all covering more than 30 km. Again, as noted earlier, there is a marked preponderance of N – S and NNW – SSE over E – W movements, the latter being virtually confined to the area south of the Voi River. In many cases the long-distance movements appeared to occur in fairly direct response to local rainstorms (cf. Fig. 3 in Leuthold and Sale 1973). The irregular distribution of rainfall, both in space and in time, made it impossible to predict such movements, but in the majority of cases the "target area" had received rain a few days previously. This was often to striking that it suggested a still unexplained ability of the elephants to sense local rainstorms over considerable distances, even against the prevailing wind.

Twenty of the 25 long-distance movements plotted in Figure 10 took place between October and January, i.e. in or near the rainy season following the long dry season. During the latter, no unusual movements were recorded in three consecutive months (July—September). The observed monthly distribution of long-distance movements deviates significantly from an assumed even distribution (Chi-square test, $p < 0.01$). A consequence of this preponderance of movements in the rainy seasons is the fact, noted above, that recorded home range sizes tended to increase "in leaps" mainly during the rainy seasons (Fig. 8).

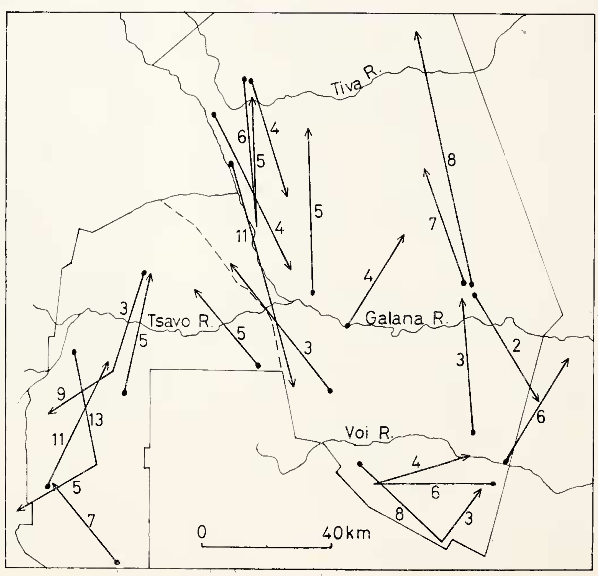

Fig. 10. Long-distance movements of radio-instrumented elephants. Figures indicate the number of days within which each movement took place

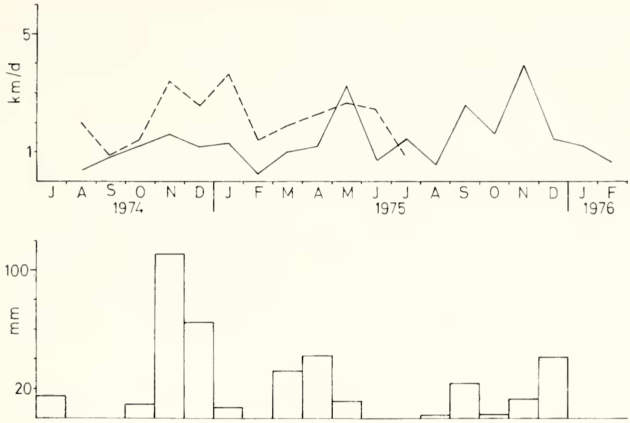

Fig. 11. Mean daily movements, in each month (see text), of ♂ M-14 (— — —) and ♀ F-17 (————) in Tsavo East *(above)*, plotted over monthly rainfall (in mm) at Sala *(below)*

All the above observations confirm the general conclusion that elephants remain relatively stationary during the dry seasons, in small dry-season ranges (Fig. 6 and 7), and move out of them mainly during the rainy seasons, or in response to out-of-season rainfall (e.g. in September 1972; LEUTHOLD and SALE 1973). In an attempt to relate movements to rainfall I proceeded as follows: For each radio-instrumented animal I determined the linear distance between every two consecutive locations and divided them by the number of intervening days, thus obtaining a — somewhat hypothetical — daily rate of movement. I then derived the mean of these values for each month of the tracking period and plotted this against monthly rainfall at a station within the home range of the elephant concerned (Fig. 11). In some — but not in all — cases the results suggest a positive relationship between monthly rainfall and the mean daily rate of movement. It is, however, rather ill-defined and correlation coefficients between the two parameters approached significance in only one case (the calculations were done only for elephants in Tsavo East, as tracking periods were too short in Tsavo West).

There are several reasons for the difficulty in obtaining quantitative relationships between mean daily rates of movement and monthly rainfall:

1. The notorious irregularity of rainfall in the Tsavo area and the relatively low density of rain gauges in the study area made it impossible to record many of the local rainstorms that apparently trigger long-distance movements. For the same reason, and also because of the large areas involved, it is difficult to decide which of the existing rainfall records the movements of a given elephant should best be related to. Thus, the actual factors influencing elephant movements are often insufficiently documented.
2. The figures designated "daily rate of movement" may not really represent true movements per day, particularly where consecutive tracking dates are a week or more apart. Two cases plotted in Figure 10 indicate what may happen during a relatively long interval: M-12 moved about 37 km in six days, then 31 km over the following fours days in almost opposite direction, ending up only 11 km from the point of origin after ten days. Similarly, F-19 was found little over 5 km from the point of departure after performing two movements of about 45 km and 40 km in six and five days, respectively. If the intervening record had not been obtained, one would have assumed that the two animals had remained

essentially stationary; the "mean daily rate of movement" obtained would have been 1.1 km/d instead of 6.8 km/d for M-12, and 0.5 km/d instead of 7.7 km/d for F-19. It is, of course, unknown how many similar cases there may have been, in which actual movements were not detected.

Thus, there is considerable qualitative evidence linking elephant movements with rainfall, but it is difficult to express this apparent relationship in quantitative terms. This would probably be easier if data collection had been more frequent and more strictly systematic for both elephant locations and rainfall records. Perhaps the ideal would be an automatic tracking system locating the animals at least once a day and a correspondingly dense network of rain gauges. Under the circumstances under which this study was carried out, this was not possible, and it may indeed be difficult to achieve anywhere under field conditions, considering the costs involved and the manpower required.

4 Conclusions and implications for management

This study was initiated to provide answers to the following questions that are important to the management of the park and its elephants:

1. What factors determine the distribution patterns and movements of elephants, and how are they reflected in the elephants' strategy of habitat utilization?
2. What is the internal organization, if any, of the Tsavo elephant population?
3. What significance, if any, do present park boundaries have for the elephants, and what is the long-term outlook, with particular reference to land use outside the park?

4.1 Strategy of habitat utilization and the influence of environmental factors

We have already identified rainfall, particularly its spatial and temporal distribution, as probably the main single environmental determinant of elephant distribution and movements (see also Cobb 1976). Of course, its influence is indirect, acting through its effect on the state of the vegetation which, in turn, provides all food for the elephants. Permanent water supplies are also important, particularly during the long dry season, the most critical time of the year; the extent to which food and water supplies are combined, or juxtaposed, locally is probably crucial for dry-season survival of the Tsavo elephants (see below).

The pattern of rainfall is relatively regular in the long term, certain parts of the year being normally dry and others wet (Fig. 2), but in the short term it is highly irregular both in space and in time (Fig. 3), producing considerable and largely unpredictable fluctuations in food and temporary water supplies. Permanent water supplies, by contrast, are generally fixed in space and thus predictable. — These ecological conditions require a strategy of habitat utilization that is geared to the long-term regularities on the one hand, yet flexible enough to accommodate the short-term irregularities on the other hand.

The main features of the elephants' long-term strategy are the relatively small localized dry-season ranges near permanent water supplies (Figs. 6 and 7) and the apparent fidelity of individual elephants to them. All radio-instrumented elephants with sufficiently long tracking periods returned to the same dry-season ranges repeatedly after "forays" into other areas during the rainy seasons. I therefore believe the dry-season ranges to be relatively immutable and knowledge on them to be maintained by tradition within the tightly knit family groups, at least in ♀♀ (whether the same applies to ♂♂ as well remains an open question).

Important components of the short-term strategy are the apparent ability of elephants to sense local rainstorms over considerable distances and their readiness

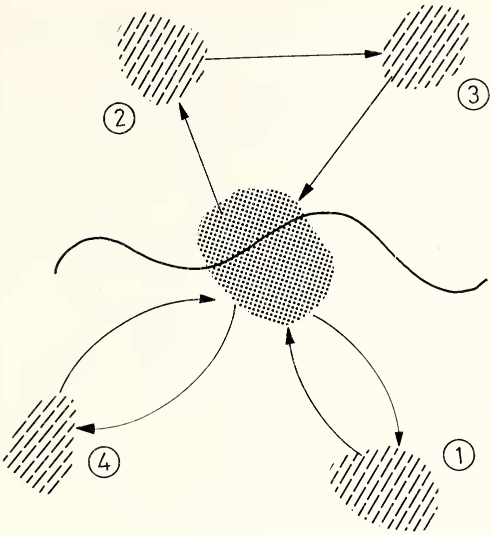

Fig. 12. Schematic representation of habitat utilization by elephants in Tsavo National Park: Movements from a fixed dry-season range (dense stippling) near a river to areas where rain (broken hatching) has fallen, and back. Figures indicate temporal sequence of local rainstorms

to move to the areas affected. We may thus view the elephants' strategy of habitat utilization as a "pulsating" system based on the dry-season ranges (stable element) and making irregular use of more distant areas where rain has fallen (opportunistic element; Fig. 12). The "pulsations" are unpredictable in timing and direction, being governed primarily by the short-term rainfall pattern. They manifest themselves as relatively long-distance movements of individual elephants (Fig. 10) and/or as large-scale shifts in overall distribution (Fig. 4). Their directions, i.e. the target areas of the elephants involved, are largely unpredictable at the onset of the rains ("outward pulsation"), but the return movements can be predicted with considerable accuracy, if individual dry-season ranges or the overall dry-season distribution pattern are known from earlier observations.

This highly flexible system of movements to and from a fixed base enables the elephants to make use of resources that are available only temporarily (rainy seasons, out-of-season rainfall), while at the same time reducing their impact on the areas on which they depend for dry-season survival.

These areas have already been adversely affected by the activities of elephants who have gradually denuded the vicinity of permanent water supplies of much of the original vegetation, particularly trees. As a result, parts of the traditional dry-season ranges no longer contain food resources sufficient to sustain the elephants using them. As elephants apparently require a certain proportion of woody plants in their diet (e.g. Laws, Parker and Johnstone 1975), they are forced to move farther and farther "inland" from the rivers in search of suitable food. This is most evident along the lower Galana River (within the park). For instance, during the long dry season of 1973 radio-instrumented ♀ F-13 (Fig. 7) was located most often some 20–25 km north of the Galana River, but occasionally at the river as well. This presumably indicates that, while she had to drink from time to time (exact frequency unknown), she did not find sufficient food near the river and had to move "inland" for considerable distances. The additional energy expenditure imposed by extensive movements between feeding areas and drinking places, throughout a long dry season, is probably crucial in the context of population regulation through mortality, both adult and juvenile (see Leuthold 1976b). This view is supported by the findings on spatial distribution of elephant carcases during the 1970/71 drought

(Fig. 4 in Corfield 1973): the great majority was found near permanent water supplies, indicating that the animals had died of starvation while water supplies still exceeded requirements.

Outside the dry season, local food quality is probably the major determinant of elephant distribution and movements. Numerous qualitative observations indicated that elephants moved into areas where rain had fallen recently and where plants were in a growing state. They appeared to be particularly attracted to areas of dense green grass under such conditions and fed extensively on grasses, at least temporarily. This is in line with findings from several food habits studies elsewhere, indicating that elephants eat large amounts of grass in the wet season, even if they appear to prefer browse at other times (Buss 1961; Field 1971; Laws et al. 1975). These impressions are supported to some extent by the analysis of the data from the monitoring flights: outside the park elephant distribution was positively correlated with either grass cover or green condition of grass, whereas inside the park no clearcut correlation with these parameters emerged (Cobb 1976).

A further point concerns the main direction of elephant movements. As pointed out earlier (cf. Figs. 5 and 10), most major movements took a N – S direction, except in the area south of the Voi River, where E – W movements were more frequent. Probably, this is mainly a consequence of the geographical accident that the major rivers in Tsavo run generally W – E (Fig. 1); elephants tend to concentrate along the rivers in the dry season and move away from them, at very approximately right angles, during the rainy seasons. This has led to a secondary zonation of the vegetation, in terms of density of woody cover which increases as one goes away from the permanent rivers. The area south of the Voi Rivers is generally less heterogeneous in terms of soil and vegetation types and has several sources of water scattered almost throughout (Fig. 1). Local rainstorms sometimes develop near Voi, due to the proximity of the Taita Hills, and fairly often in the extreme east as extensions of the coastal rain belt (see below). All this results in sometimes substantial shifts of elephants along an approximate E – W axis.

The movements to and from the dry-season ranges are often accompanied by changes in mean group size, which tends to be higher in the wet than in the dry season (Leuthold 1976a). In the dry season, while the population as a whole is concentrated near permanent water supplies (Fig. 4), actual groups within these concentrations are generally small. This decrease in mean group size in the dry season may be a mechanism reducing intragroup competition for food at a time of general food scarcity.

4.2 Internal organization of the Tsavo elephant population

From repeated aerial surveys Laws (1969a) concluded tentatively that the Tsavo elephants were subdivided into ten fairly discrete "unit populations" characterized by different biological parameters (e.g. calving rates, mean group size), inhabiting entirely separate ranges and performing only limited seasonal movements (20–30 km). Subsequent research has cast doubt on the validity of this hypothesis (Leuthold and Sale 1973; Leuthold 1976a), and the results of the present study do not support it either. A subdivision of the overall elephant population into local subunits could possibly be envisaged for the dry season, when elephants adhere to apparently fixed and probably traditionally determined ranges. However, the spasmodic and unpredictable wet-season movements can bring elephants from quite different dry-season ranges into contact, so the social and/or reproductive identity of possible subunits may be lost, at least temporarily (cf. Fig. 6 in Leuthold and Sale 1973). For example, the ♀♀ F-12 and F-14 (Fig. 7) were both captured in their respective dry-season ranges, F-12 somewhere near Voi (not shown in Fig. 7, as there were too few records) and F-14 near Sala, some 60 km away. A few months later, after some rain had fallen, they were both found near the point where the Voi River leaves the park in the east, only about 10 km apart. Similarly, ♂♂ M-4 and M-7 moved from their presumed dry-season ranges in southern Tsavo West into the northern portion, when rain had fallen there (Figs. 6 and 10), confirming our ealier suspicion that the elephant populations of southern and northern Tsavo West were not discrete entities as implied by Laws' (1969a) hypothesis (the suspicion was based on the earlier movements of M-3; see Fig. 2 in Leuthold and Sale 1973). Unfortunately, no corresponding data are available on ♀♀ of that area.

The converse occurred, too, i.e. animals with overlapping dry-season ranges moving to very different areas in the wet season. In mid-May 1975, ♀♀ F-18 and F-19 were over 100 km apart (southern- and northernmost records, respectively, in Fig. 7) under at least partly green conditions. By September they had moved into overlapping portions of their dry-season ranges and were found only 10—15 km apart.

In this context it must be emphasized again that radioinstrumented elephants — and some visually identified ones, too — moved over considerably greater distances (see Table 4) than Laws (1969a) anticipated. Their movements were, however, not unprecedented, as evidenced by the observation by Parker (in Laws et al. 1975, p. 16) of some 2.000 elephants moving over a distance of about 100 km within six months in the north-east of the present study area (Galana Ranch). At the same time, the results of this study, particularly those indicating adherence to relatively fixed dry-season ranges, lend little credence to earlier reports of annual elephant movements over several hundred km, e.g. from Mount Kilimanjaro to the Lorian Swamp in north-eastern Kenya and back (Sikes 1971).

The above information on the spatial structure of the Tsavo elephant population is important for future research and management. Any operations for which localized effects, repeatability and/or a degree of predictability are desired (e.g. local sampling of live or dead animals, capturing and marking of individuals), are best carried out in the dry season, when largely the same elephants can be expected to be in the same areas. By coincidence, the dry season is also the best time for field work, particularly on the ground, from the practical point of view (accessibility of different areas, cross-country driving, etc.). Use has already been made of these suggestions in 1. capturing elephants for radio-tracking mainly in the dry season (so as to have an indication of their dry-season range from the start), and 2. repeated aerial photography of elephants to determine age structures in — presumably — the same "subpopulations" (Leuthold 1976b).

Another point of interest in this context is the repeated formation of large to very large herds of elephants in some areas. In almost every wet season, herds of several hundred animals (1.100 in May 1974) formed in the southeastern corner of Tsavo East near, and sometimes outside, the park boundary. Similar aggregations were observed by Laws in the same area in 1967 and stated to exist throughout the year (Laws et al. 1975, p. 105). The latter certainly did not apply during the present study; as the vegetation dried up, the large herds gradually dissolved again and, at the height of the dry season, hardly any elephants could be found in the area concerned (which does not have any permanent water supply). Laws has repeatedly drawn attention to such large herds, which he interpreted as resulting from disturbance by humans at the periphery of the elephants' range (e.g. Laws et al. 1975, pp. 100—105). While this may apply to some situations in Uganda (cf. Eltringham 1977), it almost certainly does not in Tsavo, since — apart from the purely seasonal nature of the aggregations there — similar herds have been observed from time to time in other areas of the park (generally in the wet season, too), but not in places where human disturbance could easily be envisaged as a causative factor (cf. COBB 1976). On the basis of the present study and some additional observations I offer the following tentative explanation for the formation of these seasonal "super-herds":

Tsavo East receives most of its rainfall from cloud formations moving inland from the coast. This is evident both from subjective experience and from the fact that isohyets in south-eastern Kenya run approximately parallel to the coast (National Atlas of Kenya 1970, pp. 15—17; COBB 1976). As a result, the easternmost portions of the park are often the first to receive substantial rain at the beginning of a rainy season, or even out of season occasionally. After a long, nutritionally severe dry season, such local rainfall and the consequent plant growth can attract elephants over considerable distances (perhaps 30—50 km). As the vegetation in the area concerned happens to be mainly open grassland, which tends to favour aggregations both in elephants (LEUTHOLD 1976a) and in other ungulates (e.g. LEUTHOLD 1977), formation of large herds is to be expected. These herds may eventually move into more wooded areas, where they are likely to fragment. As rain falls in other areas, or as the vegetation dries up, the elephants then move elsewhere and/or disperse again (cf. Figs. 4 and 5 in LEUTHOLD and SALE 1973).

Within the aggregations described here, relatively intensive mating activity has been observed repeatedly. This may be a consequence of the particular social situation in the aggregations or of the favourable environmental conditions prevailing at those times, or perhaps of a combination of both. Possibly, this recurring phenomenon is a major cause of the — not very marked — seasonality in the reproduction of Tsavo elephants (LAWS 1969b).

4.3 Present park boundaries and future outlook

With an area of 20.000 km² Tsavo National Park is undoubtedly a very important wildlife sanctuary, both for elephants and other animals. Nevertheless, experiences in earlier elephant counts (LEUTHOLD 1973) and the results of the present study (including the work of COBB 1976) clearly show that Tsavo elephants utilize large areas outside the present park boundaries. In particular, much of the wet-season dispersal area lies outside the park, especially in the north-east and, to a lesser extent, in the south-east (Fig. 4). Several of the radio-instrumented elephants were repeatedly recorded outside the park, mainly in the Sala area (M-14, F-14, F-17; Figs. 6 and 7), but also around the Taita Hills (M-15, M-6, M-7; Fig. 6) and west of the Athi River (F-18; Fig. 7).

This presumably means that the park's resources are insufficient to sustain, the year round, the elephants currently using it, and/or that certain elephants still utilize areas that they know through tradition but which happen to be outside present park boundaries. In either case the future of the elephants involved depends largely on future land use in the areas concerned and thus appears somewhat tenuous. Kenya's human population has been increasing at a rate of over 3 % p.a. in recent years, and any land not currently protected for wildlife conservation or a similar purpose is likely to come under increasing pressure to be used for ranching, agriculture and settlement. Since elephants and people do not mix well, the potential for conflict is considerable, and elephants may eventually be displaced from many areas they still utilize at present.

This has already happened locally, for instance in the area between the Athi River and the Mombasa-Nairobi road (Hunting Block No. 29), just north and west of present park boundaries (Fig. 1). Until about 1965/66, this area was virtually uninhabited by humans. The tarmacking of the road in 1967, coupled with the general demand for land, led to fast-increasing settlement in that area. As a consequence, elephants have been largely forced to withdraw, as reflected by the results of two total counts: 565 elephants in 1965 versus 7 in 1972 (Leuthold 1973). During the monitoring flights of 1973–74 elephants were hardly ever seen in the area in question, whereas smaller ungulates still existed in some numbers. Several records of radio-instrumented ♀ F-18 (Fig. 7) show that elephants still occasionally venture into that area, but only at great peril, as evident from the numerous carcases and skeletons seen there from the air (Cobb 1976).

Fortunately, the outlook is not as bleak in some of the other areas around the park. On the Galana Ranch, adjoining Tsavo East north of the Galana River (Fig. 1), a long lease enables a multiple land-use system to be practised, in which wildlife conservation and limited commercial exploitation play a prominent role. Elephants have virtually unlimited access to the entire area (cf. Fig. 4 in Leuthold and Sale 1973) and are discouraged only where they damage installations for cattle (e.g. watering points).

The area north of the Galana Ranch, important for wet-season dispersal of Tsavo elephants (Fig. 4), is largely unsuitable for human use other than the present seasonal utilization by nomadic pastoralists, mainly on account of its low and erratic rainfall (see data in Cobb 1976). As far as can be foreseen at present, this area is therefore likely to be available and accessible to elephants, at least seasonally, for some time to come.

The same cannot be said of most areas adjoining southern Tsavo East to the east and south. Their slightly higher rainfall makes them potentially suitable for cattle ranching, and large areas between the southern parts of Tsavo East and West are currently being developed along these lines. Since free-roaming elephants are not readily compatible with such developments, they may eventually be denied access altogether. This would result either in a reduction of the overall elephant population (if the elephants concerned were simply eliminated), or in an increase in elephant density inside the park (if they were merely displaced). In the latter case, a reduction in available wet-season dispersal areas would increase pressure on the already overutilized vegetation within the park.

Important conclusions for park management from this and the preceding sections are as follows:

1. The park in its present boundaries cannot support all elephants in the Tsavo ecosystem (as defined by Cobb 1976) the year round.
2. Tsavo National Park is not (yet?) – as some other parks – an "island in a sea of human settlement", but its elephants, in particular, depend on unhindered access to some adjacent areas, especially in the rainy seasons.
3. Increasing human settlement around the park will initially reduce mainly the wet-season dispersal areas; the consequences of this may not become evident in the park until some time afterwards.
4. As a consequence of the above, numbers and distribution patterns of elephants (and other game), as well as human activities around the park, should continue to be monitored at regular intervals, along the lines of the program described by Cobb (1976).
5. As a corollary to the above (4.), the national park authorities should endeavour to be informed, and even consulted, on major decisions concerning the land use in areas adjacent to the park.

Of course, there are other factors affecting the welfare of Tsavo National Park and its elephants, the most important of which is probably poaching and the degree to which it can be brought under control. However, this is outside the scope of the present paper, dealing with the habitats in and near the park and the elephants' ways of using them.

Acknowledgements

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Summary

In the context of the "Tsavo elephant problem" this study was undertaken to provide information on movements and home ranges of elephants and on their strategy of habitat utilization. Visually identified individuals were located repeatedly, and some 20 elephants were radio-tracked for periods of 2—37 months. Individual home ranges measured 400—3.700 km², with means of 750 km² in Tsavo West and 1.600 km² in Tsavo East. Home range diameters varied from 25 to 133 km, with means of 51 km in Tsavo West and 73 km in Tsavo East. The differences between Tsavo East and West are attributable to environmental conditions, which are more favourable and more stable in Tsavo West. During the dry seasons, elephants occupy relatively small ranges near permanent water supplies, from which they move to areas where rain has fallen early in the rainy seasons. Apparently they are able to sense local rainstorms over considerable distances. Major movements thus occur primarily during the rainy seasons. These findings agree with those on seasonal changes in overall distribution patterns, determined by repeated aerial sample counts. Seasonal ranges and movements appear to be determined primarily by the food and water supplies available which, in turn, depend mainly on rainfall. The irregular distribution of the latter, both in space and in time, necessitates a highly flexible strategy of habitat utilization. The results of this study do not support an earlier hypothesis on the internal subdivision of the Tsavo elephant population into about ten discrete units. At present, Tsavo elephants still utilize large areas outside the park, at least seasonally. If future changes in land use make these areas inaccessible to elephants, this could have grave consequences for the park. Continued monitoring of elephant populations and their distribution patterns, and of human activities outside the park, is therefore indicated.

Zusammenfassung

Wohngebiete und Wanderungen afrikanischer Elefanten im Tsavo-Nationalpark, Kenia

Die vorliegende Untersuchung ist ein Teil der Forschungsarbeiten zum „Elefantenproblem" im Tsavo-Nationalpark. Wiederholte Ortung von über 20 mit Radiosendern versehenen Elefanten während 2—37 Monaten ergab individuelle Wohngebiete von 400—3700 km². Im Ostteil des Parks waren sie größer (Mittel 1600 km²) als im Westteil (750 km²), ebenso ihre Durchmesser (Ost 73 km, West 51 km), die 25—133 km betrugen. Diese Unterschiede lassen sich auf die Umweltbedingungen zurückführen, die im Westteil insgesamt günstiger und stabiler sind. Während der Trockenzeiten halten sich die Elefanten in relativ kleinen Einständen in der Nähe permanenter Wasserstellen auf, von denen sie zu Beginn der Regenzeiten „ausschwärmen" in Gebiete, in denen Regen gefallen ist. Sie scheinen lokale Regenfälle aus größerer Entfernung wahrnehmen zu können. Bedeutende Ortsveränderungen

(30—50 km und mehr in wenigen Tagen) erfolgen daher vorwiegend in den Regenzeiten. Diese Befunde stimmen mit dem Bild überein, das sich aus großräumigen Veränderungen der örtlichen Verteilung der Elefanten ergibt (durch Luftzählungen ermittelt). Die saisonalen Wohngebiete und die unregelmäßigen „Wanderungen" sind vorwiegend durch das Angebot an Nahrung und Wasser bestimmt, das seinerseits hauptsächlich von den Niederschlägen abhängt. Deren Unregelmäßigkeit — zeitlich wie örtlich — bedingt eine flexible Strategie der Biotopnutzung. Eine frühere Hypothese zur Unterteilung der Tsavo-Elefantenpopulation in etwa zehn getrennte Einheiten konnte nicht bestätigt werden. Zur Zeit benützen die Tsavo-Elefanten noch größere Gebiete außerhalb des Nationalparks. Falls diese durch menschliche Besiedlung für die Elefanten unzugänglich werden, können sich daraus für den Park ernsthafte Probleme ergeben. Fortdauernde Überwachung des Elefantenbestandes und seines Verteilungsmusters sowie der menschlichen Aktivitäten außerhalb des Parks ist daher angezeigt.

References

NATIONAL ATLAS OF KENYA (1970): 3rd ed. Nairobi: Survey of Kenya.

AYENI, J. S. O. (1975): Utilization of waterholes in Tsavo National Park (East). E. Afr. Wildl. J. **13**, 305—323.

BUSS, I. O. (1961): Some observations on food habits and behavior of the African elephant. J. Wildl. Manage. **25**, 131—148.

BUSS, I. O.; SMITH, N. S. (1966): Observations on reproduction and breeding behavior of the African elephant. J. Wildl. Manage. **30**, 375—388.

COBB, S. (1976): The distribution and abundance of the large herbivore community of Tsavo National Park, Kenya. D. Phil. Thesis, Univ. Oxford.

CORFIELD, T. F. (1973): Elephant mortality in Tsavo National Park, Kenya. E. Afr. Wildl. J. **11**, 339—368.

DOUGLAS-HAMILTON, I. (1972): On the ecology and behaviour of the African elephant. — The elephants of Lake Manyara. D. Phil. Thesis, Univ. Oxford.

ELTRINGHAM, S. K. (1977): The numbers and distribution of elephant *Loxodonta africana* in the Rwenzori National Park and Chambura Game Reserve, Uganda. E. Afr. Wildl. J. **15**, 19—39.

FIELD, C. R. (1971): Elephant ecology in the Queen Elizabeth National Park, Uganda. E. Afr. Wildl. J. **9**, 99—123.

GLOVER, J. (1963): The elephant problem at Tsavo. E. Afr. Wildl. J. **1**, 30—39.

LAWS, R. M. (1969 a): The Tsavo Research Project. J. Reprod. Fert., Suppl. **6**, 495—531.

LAWS, R. M. (1969b): Aspects of reproduction in the African elephant *Loxodonta africana*. J. Reprod. Fert., Suppl. **6**, 193—217.

LAWS, R. M.; PARKER, I. S. C.; JOHNSTONE, R. C. B. (1975): Elephants and their habitats. — The ecology of elephants in North Bunyoro, Uganda. Oxford: Clarendon Press.

LEUTHOLD, W. (1969): Naturschutzprobleme und ökologische Forschung in Ostafrika. Schweiz. Naturschutz **35**, 117—125, 150—153.

— (1973): Recent elephant counts in Tsavo National Park. Voi/Nairobi: Mimeographed report.

— (1976 a): Group size in elephants of Tsavo National Park and possible factors influencing it. J. Anim. Ecol. **45**, 425—439.

— (1976 b): Age structure of elephants in Tsavo National Park, Kenya. J. Appl. Ecol. **13**, 435—444.

— (1977): African ungulates. — A comparative review of their ethology and behavioral ecology. Berlin - Heidelberg - New York: Springer-Verlag.

LEUTHOLD, W.; SALE, J. B. (1973): Movements and patterns of habitat utilization of elephants in Tsavo National Park, Kenya. E. Afr. Wildl. J. **11**, 369—384.

NAPIER BAX, P.; SHELDRICK, D. L. W. (1963): Some preliminary observations on the food of elephants in the Tsavo Royal National Park (East) of Kenya. E. Afr. Wildl. J. **1**, 40—53.

SIKES, S. K. (1971): The natural history of the African elephant. London: Weidenfeld and Nicolson.

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